

Report on
COLUMBIA BASIN OLIGOCHAETA

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COLUMBIA BASIN OLIGOCHAETA
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Earthworms (megadrile oligochaeta) of the eastern Columbia River Basin

This section of the report summarizes the earthworm information available in published literature. I have presented the material in an item-by-item fashion, according to the nine items described in the contract specifications.

Item 1. Species of special concern to land managers

The CRB is inhabited by at least three native earthworm species, belonging to three genera. All three ought to be of special' concern. One, *Driloleirus americanus*, was considered for inclusion in the IUCN Invertebrate Red Data Book because its habitat was threatened and its range was not known to be very large. It is itself rather large for a worm. The currently available information suggests that it may be a narrow endemic utilizing a threatened habitat (shrubland sites with good soil). The collection data do not give much detailed information on habitat type. The three sites (near Pullman and Ellensburg, WA and Moscow, ID (Fender and McKey-Fender 1990) are located in what is now agricultural land, grassland and shrubland (CRB 001, 002).

The other two native species, *Drilochaera chenowithensis* and *Argilophilus hammondi*, may be somewhat tolerant of habitat disturbance. Their type localities were on uncultivated canyonland surrounded by orchards (McKey-Fender 1970). Though they may therefore be considered more likely to survive, I would still recommend that special

attention be given them. In particular, learning more about their ranges and ecological flexibility would enable land managers to determine whether or not special measures are necessary.

In general, native species earthworms are vulnerable to habitat disturbance and invasion by exotic species. When the unprocessed collection information of W. Fender and McKey-Fender is brought to light, there may be many more native species known for the CRB. Alternatively, survey efforts could be launched to complement and/or duplicate their work, in the event that collaboration is not possible. In the meantime, one must remain aware that a large number of exotic “weedy” earthworm species is present in the CRB (as well as all other parts of the USA). These species may be able to outcompete endemics. Replacement of endemics by exotics has been observed in many parts of the world, including northern California (Eisen, 1900), Illinois (Smith, 1928), New Zealand (Lee, 1961), and South Africa (Ljungstrom, 1972). In many of these cases the guilty worms are the same species as present in the CRB.

This leads to another area of concern to land managers: invasion by exotic species. The foreign earthworms present in the CRB are (so far) all members of the family Lumbricidae and with one rare American exception (*Bimastos parvus*) are of European origin. These are the worms with which the average American is most familiar. This invasion is a cause for concern for two reasons. The first has already been mentioned- these worms may reduce or eliminate populations of native species. Generally this occurs concurrently with habitat destruction or fragmentation (Kalisz and Dotson, 1989). It appears that large areas of intact habitat are somewhat more resistant to native species loss, though the long term outcome is not known.

The second ‘reason for concern arises in regions where native earthworms do not occur. This absence may be for many reasons, among them glaciation, long dry periods, isolation from potential colonists by intervening deserts, etc. Soil and litter development in the absence of worms is very different from in the presence of worms, particularly in forest ecosystems (e.g. Langmaid, 1964). There may be corresponding differences in the nutrient cycling dynamics, soil mesofauna, soil

microfauna and soil microflora of worm-free and worm-inhabited systems. With the introduction of earthworms, soils can be greatly altered. I have observed this in northern lower Michigan. I would not be surprised to see similar effects in western forests.

Do land managers wish to maintain worm-free areas in their natural state? Is it important to maintain native species, or for larger purposes of sustainable land use, is any worm good enough? Efforts to control the spread of exotic earthworms may be futile, and there is not enough information about the relative ecological impact of native and exotic species to inform a policy decision about how to manage earthworm biodiversity.

Item 7. Special habitats

The only obvious special habitat is that of *Driloleirus antarcticus*, known from the native shrublands of eastern Washington and western Idaho. I have some recollection that the native vegetation of this region is scarce, and it is not known if the worm survives habitat conversion to agriculture. There is not enough information on other native species to tell if any others are similarly limited by habitat conditions.

Item 6. Biogeography

The location of *Driloleirus antarcticus* has been discussed in two places above. *Drilochaera chenowithensis* is known from only one site along the Columbia River at Chenowith Creek, west of The Dalles (McKey-Fender 1970). *Argilophilus hammondi* has been found at the Chenowith Creek site, well to the south in the Ochoco National Forest "above Prineville" in an open Ponderosa pine forest with sedges and grasses in the understorey, and at a site "above Grant Meadows, elevation about 5000 feet" (McKey-Fender 1970). Fender (pers. comm.) gives the location as on the slopes of Grant Butte in Crook County. Vegetation was "open, park-like forest of yellow pine, white fir..." with a sparse ground cover (McKey-Fender 1970).

The native species of the CRB belong to genera with other species on the west side of the Cascades. Some genera have ranges extending well to the south into California. *Argilophilus* is the most southerly, with a limit

near the latitude of Riverside, California (Wood and James 1993). The closest related genera to the Pacific Coast earthworm fauna are in Australia and Burma (Gates 1977).

Given the scanty information, it is not possible to identify areas of high diversity or endemism. It is generally true that earthworms show low within-site diversity, with 3 to 6 species per site, but high diversity among sites. This is because in topologically complex land areas, many species have limited distributions. For example, New Zealand has roughly 200 species of earthworms, but seldom are more than 4 found in any one spot (Lee, 1959). Fender (pers. comm.) estimates the Pacific coast earthworm fauna to contain 80-100 species, all but 20 or so undescribed. The majority of the described species (all but three) are from the west slope of the Cascades and Sierra Nevada. Since collector bias would favor the wetter areas, one would not hasten to conclude that published species descriptions are a random sample of the total possible. Fender (pers. comm.) indicates that five genera are represented in the CRB area: *Driloleirus*, *Drilochaera*, *Argilophilus*, *Arctiostreptus* and *Macnabodrilus*. However half of the species have not been described.

Forest Service and BLM lands, particularly the former, are likely to harbor the majority of surviving native earthworm species populations in the CRB. Interior Ponderosa pine and Douglas fir forests and other non-xeric habitats probably support the native species. FS/BLM lands near fishable streams or human settlements may also harbor exotic species. The Steens Range, bitterbrush areas, juniper stands and sagebrush are thought to lack earthworms (Fender, pers. comm.). Fender suggests that native species tend to be favored by fine-textured soils, while Lumbricidae can invade more easily in coarse-textured soils.

Among non-FS/BLM land areas, I would suggest that riparian zones, and privately owned grazing land and timber are most likely, to harbor native and introduced earthworms. Agricultural land, particularly dryland farms are less likely.

Item 3. Habitat requirements, sensitivity to disturbance, and population trends for selected species within designated habitats.

Earthworms have been recorded from sites within the following habitat types, according to the map and where available, collection data: SAF 206, 210, 213, 218, 237; SRM 107, 109, 110, 304, 607; CRB 001, 002, 004. Habitat requirements for most earthworms are probably very similar over the vegetation types: moist soil between 0 and 25 °C for at least 3-4 months per year and neutral to slightly acid soil pH (cf. Lee 1985). Details of habitat requirements, sensitivity to disturbance and population trends are unknown for all the native species (see Item 1). However, collection data from Fender and McKey-Fender (unpublished) would suggest that virtually any disturbance that alters vegetation or allows the entry of exotic species has the potential to reduce or eliminate native species populations. Since their observations are not based on experimental manipulations, it would be difficult to define the necessary or sufficient conditions for native species elimination. The unanswered question here as in all other cases of exotic earthworm invasions is the degrees to which habitat disturbance and ecological competition contribute to the replacement process.

The exotic species from Europe have achieved their current global temperate zone distribution due to their broad adaptability to different habitats and their resilience following disturbance. Population trends are unknown. New populations are probably being founded. It is likely that populations are expanding in numbers and geographic extent as individual movements (basically a diffusion process) enlarge the occupied territory.

It is very likely that additional CRB map area vegetation cover classes are inhabited by earthworms. CRB 003, SAF 217, SAF 235, SRM 103, SRM 36 and SRM 402 are good candidates.

Item 4. Factors determining distribution and abundance of earthworms in designated habitat types

Earthworms require organic matter in various stages of decay and in various locations. Three broad functional groups of earthworms have been described by Bouche (1977): epigeic, endogeic and anecic. Epigeic worms

are typically small, darkly pigmented, and reside in leaf litter layers and under the bark of decaying logs. They have high rates of reproduction and short life spans. Endogeics live in the mineral soil and consume organic matter within the soil or at the soil-litter interface. They are larger, less pigmented to unpigmented, have longer lives and lower reproductive rates. Anecics are those that inhabit a permanent or semi-permanent deep vertical burrow and emerge at night to consume relatively fresh plant detritus on the surface. These are the largest and longest-lived earthworms. Lavelle (1983) has further divided the endogeic category into polyhumic, mesohumic and oligohumic types. Polyhumic endogeics work on richer sources of organic matter closer to the soil surface or at the soil-litter interface, while the others live successively deeper in the soil and on more finely divided or decomposed organic matter. Structures to increase gut surface area are most highly developed in the oligohumic endogeic species, and least developed in epigeics and anecics.

The status of the three native species is unclear, though they are probably all endogeics. Among the exotic species, *Lumbricus terrestris* is anecic, *Dendrobaena rubida* and *Bimastos parvus* are epigeic, and the rest are endogeic. The *Aporrectodea* spp may be best considered meso- or polyhumic endogeics. *Eiseniella tetraedra* has a life history resembling the epigeics, but it is semi-aquatic.

Down woody debris (logs, large branches) are a key environmental factor for the epigeic species known from the CRB. Consequently a stand must be old enough to produce such material. Generally a log of 10 cm diameter will have sufficient bark and decomposing cambial layers to support these worms. However, the 'stage of decay is important. A steady supply of logs reaching the state in which the bark is loose but not yet falling off, and in' contact with the ground, is necessary to maintain a population. Therefore an even-aged young stand of trees is not likely to supply this resource. Consequently, another key environmental factor could be stand age and/or stand age diversity.,

Tree species in the stand may also be important. My experience in eastern forests is that log specialists are less likely to be encountered in oak and conifer logs, and more often found in other broadleaved species,

such as maple, birch, aspen, tulip poplar, cherry, etc. Similar relationships may hold in the west also.

These worms can exist between logs if the litter is sufficient. Another key factor would be leaf litter depth. It must be sufficient to **provide** moisture retention in the lower layers of the litter between rains, so that the worms can feed on the litter. My educated guess is that 3-6 cm of litter and humified organic matter is a safe minimum. Since these worms are very active they can find deep litter accumulations and woody debris, provided the moisture regime is favorable.

A fourth key factor would be the moisture regime. Downed woody debris and deep litter are of no use if these resources are not wet long enough each season.

No empirical data are available to quantify the contribution of each factor to the distribution and abundance of these species. My best guess is: logs 0.1, tree species 0.1, litter depth 0.4, moisture regime 0.4.

Bimastos parvus was found in SAF 206 under logs and stones , while *Dendrobaena rubida* was found in a riparian area within CRB 001 (Gates, 1967).

Anecic species are represented (*so far*) by *Lumbricus terrestris* (a.k.a. nightcrawler). It was recorded from two artificial environments, a lawn of the University of Idaho and in a roadside picnic area near Pocatello (Gates 1967). The species can live in. forested or **grassland/shrubland** areas provided it can escape deep into the soil when surface or **near-**surface temperatures go much above 15-20 C. It is known to prefer , leaf litter low in tannins, e.g. rejecting oak in favor of maple. Further comment on this species seems unwarranted until it is found within natural habitats of the CRB. *Driloleirus americanus* may also be **anecic**, based on its deep burrowing habits and largely organic diet.

The endogeic species (**including** native and exotic) occurred in a wide range of habitats- SAF 210, 213, 218, 237; SRM 107, 109, 110, 304, 607; CRB 001, 002, 004. Lumping these into three categories will simplify the rest of this section: forest and Savannah, **grassland/shrubland** (including exotic grass pasture and seral stages following cessation of agriculture), and cultivated land. This act of lumping will reduce the number of times I

will have to say "I don't know".

Endogeic species are the least well known of all earthworms, even though they are the majority. This is because their lifestyle is not so obvious. The fraction of the soil organic matter on which a given species feeds is known only for a very few species, and none of the ones present in the CRB.

The native species are completely unknown as regards factors influencing their populations. Only by assuming them to be comparable to other earthworms can one say that soil moisture, soil temperature, organic matter quantity and quality, and soil pH are probably the most important factors (Lee 1985). However, we have already narrowed the consideration to specific habitat types, and those probably fall within the limits of tolerance of most temperate zone endogeic earthworms. This leaves us with the task of examining the influences of variations of these factors within the ranges of tolerance.

Soil climate determines the periods of activity during the year, their timing and duration. Within a habitat type, there will be variations in soil climatic factors (due to slope, aspect, soil particle size distribution, drainage characteristics) and thus some variation in earthworm activity period and perhaps abundance. Forested habitats appear to be the ones with the most buffered soil climate. Perhaps soil climate is not as important a limiting factor in forest as it is in more exposed circumstances such as grasslands and agricultural land. Grassland temperature and moisture regimes are generally more extreme and will accentuate the effects of slope, soil type, etc. If the agricultural cycle includes long periods of bare ground, this can further magnify the impact of weather on worms.

Organic matter can be supplied to the endogeics from above or from root deposition. There may be species differences in dependence on these sources of organic matter, and there are differences in quality of organic matter from these two sources. Unless the organic matter of a habitat renders the soil strongly acid, organic matter quality is probably not a major factor affecting endogeic earthworms, within the normal range of most ecosystems composed of perennial vegetation.

Quantity of organic matter is generally a significant limiting factor

for earthworms. Since most agricultural soils are depleted of, organic matter, this is likely to be a strong influence in ag land or recently abandoned ag land. However, since I have no idea what the organic matter levels in the soils of the various cover types are, nor any information on critical levels for any of the native or exotic species, it is not possible to make a firm statement about the importance of organic matter quantity to earthworm abundance in natural vegetation types of the CRB.

Soil pH is often cited as a limit to the establishment of earthworms in boreal forests or other acid soils. If any of the higher elevation forests have this characteristic, earthworms may be restricted from those sites. With no pH or soil data from the cover types or from most of the worm collection data, I cannot make informed judgements. However, some Pacific coast **endemics** are tolerant of acid soils (pH 3.1-5.0; McKey-Fender et al 1994), leaving open the possibility that limitation will be less important than for the Lumbricidae. Even so, the acid soil-tolerant species are from the west slope of the Cascades, so even this is speculative. The endogeic species present in the CRB are mostly exotics with proven abilities to handle wide variations in soil conditions, such as *Aporrectodea trapezoides*. The native species are totally unknown. *Argilophilus hammondi* was collected from two Ponderosa pine sites of pH 5.5 and 6.0, values tolerable to almost any worm on the planet.

To summarize the above lack of definitive information, I will give my best guesses about the relative contributions of the various factors in the three lumped cover types. In forest/Savannah: moisture 0.2, temperature 0.2, organic matter 0.4, pH 0.2. In shrubland/grassland: moisture 0.4, temperature 0.3, organic matter 0.2, pH 0.1. In cropland: moisture 0.3, temperature 0.3, organic matter 0.35, pH 0.05.

Item 5. Functional roles of earthworms.

Functional roles will vary more among ecological types of earthworms than they will among habitat types. If a habitat type does not support a certain ecological category, then any functional role unique to an earthworm category will be missing from that habitat.

Anecic earthworms are unknown from natural vegetation in the CRB.

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Their unique contributions would be the transfer of relatively fresh plant litter from the surface to deep levels of the soil and the creation of deep vertical burrows which assist water infiltration. Other earthworm types can contribute to these processes but not in as direct and effective a manner. Anecics also provide food resources to endogeic worms by deposition of fecal organic matter in the soil where endogeics can reach it.

Epigeic worms are known from two sites in the CRB, one in SAF 206 within the Grand Teton National Park, and the other from a riparian area within CRB 001. In a forested site epigeics would be expected to have the following key functional roles: 1. organic matter comminution- by reducing the size of organic matter particles during passage through the worm, the OM is made more accessible to action by other decomposers; 2. nutrient cycling- these earthworms will digest organics and thus mineralize some of the nutrients bound in them. All earthworm **excreta** have higher levels of available macronutrients and cations than the material ingested (see review in Lee 1985). Urine is a source of available N, and body tissues readily decompose on death; 3. soil structural modification- the acts of burrowing and defecation create soil structures potentially significant (though the details are unknown anywhere) to other soil biota. The soil structures created are hydrologically significant and soil water-stable aggregation is promoted; 4. transfer of organic matter to the soil- consumption of surface litter results in some defecation in the mineral soil, particularly if worms retreat into the mineral soil to avoid unfavorable climatic conditions in the litter; 5. food for other animals- predators of earthworms include small mammals, beetle larvae, centipedes, some flies and birds. Quantification of the impact of predators on earthworm populations is difficult. No data on this subject are available for the USA.

Endogeic earthworms were found in SAF 210, 213, 218, 237; SRM 107, 109, 110, 304, 607; CRB 001, 002, 004. Key functional roles within non-cultivated land are probably very similar across cover types. These roles are: 1. organic matter comminution- by reducing the size of organic matter particles during passage through the worm, the OM is made more accessible to action by other decomposers; 2. nutrient cycling- these earthworms will digest organics and thus mineralize some of the nutrients

bound in them. All earthworm **excreta** have higher levels of available macronutrients and cations than the material ingested (see review in Lee 1985). Urine is a source of available N, and body tissues readily decompose on death; 3. soil structural modification- the acts of burrowing and defecation create soil structures potentially significant (though the details are unknown anywhere) to other soil biota. The soil structures created are hydrologically significant and soil water-stable aggregation is promoted; 4. soil profile development, or transfer of materials within the soil- defecation within the mineral soil will not always be at the same level as consumption. There may be **deposition** of casts on the soil surface, in which case mineral soil is being brought up to the surface, and there may be deposition of upper soil horizon material in the deeper strata; 5. soil carbon **protection**- endogeic earthworms produce fecal pellets (casts) which are water-stable aggregates, and within which soil carbon is partially protected from oxidation. Although the initial evolution of a cast includes a phase in which microbial respiration of soil carbon is enhanced, the long term effect of organic matter incorporation into casts is to slow the, oxidation of soil carbon (Lavelle and Martin 1992). In this way earthworms contribute to the soil carbon sink. 6. food for other **animals**-predators of earthworms include small mammals, beetle larvae, centipedes, some flies and birds.

In cultivated land the same functional roles apply but to lesser degrees. Roles 1-3 above are essentially the same, but the action of **tillage** equipment erases much of the structural impact. Fertilizer application has a much greater impact on plant nutrition than earthworm mineralization of nutrients. **Tillage** itself is much more important than role 4 above, the transfer of material within the soil, so the earthworm 'function will be negligible. Cultivation and fertilizer application tends' to reduce soil carbon amounts until only the most stable fractions remain. Earthworms have little impact on this refractory soil organic matter. Thus soil carbon protection in agricultural land is unlikely to be significant under conventional agricultural practices. Predation on earthworms takes place in some arable lands, and can be accentuated by turning the soil and exposing worms to bird predators. **Tillage** can act as a "predator", killing a

significant fraction of the earthworm population. In general, agricultural practices replace earthworm functional roles with mechanical and chemical inputs, and tend to reduce earthworm populations.

2. Earthworm functional group models

The models illustrated in the accompanying figures are largely graphical representations of the material discussed in Items 4 and 5. Each model is provided with a list of cover types to which it applies. ♣ Here as in Items 4 and 5 I have grouped cover types into three categories. This was done because there is not sufficient information to justify separate treatment of the cover types in which earthworms are known to occur in the CRB. For some of the key environmental correlates, or e-factors, I have indicated factors contributing to these e-factors. Readers will note that some of these **contributing** factors are not present in the GIS attributes or themes available to me, and there did not seem to be any reasonable proxies.

For each of the functional roles indicated in the models, I have assigned a numerical importance value, 5 being high and 1 being low. These are intended to reflect the significance of the function to the system modelled.

Item 8. Management scenarios and their impact on earthworms and earthworm functions

I was unable to locate any management scenarios in the packets of information received. Nevertheless, I can confidently state that nothing is known of the impact of any management practice on any CRB native earthworm species. Where a management plan changes the key environmental correlates for a group of earthworms (best to go by functional groups for the time being), one can expect some impact. In the absence of any more **specific** guidelines, I am assembling some basic information on the impact of grazing, prescribed fire and logging on earthworms.

Grazing: Effects of grazing on earthworms include at least three components: 1) manure deposition on the soil surface partly replaces leaf

litterfall, 2) root death is a consequence of grazing, and thus **rhizodeposition** of detritus in the soil is increased (up to a point), and 3) soil compaction by livestock.

From the earthworm point of view, conversion of **herbage** to manure changes the quality and accessibility of detrital material. What would have been litter is now partly predigested, may be toxic in the short term, is clumped rather than dispersed, and is highly attractive to a number of other invertebrates. James (1992) described the functional response of several earthworm species to *Bison bison* dung pats in tallgrass prairie. Species with characteristics of polyhumic endogeics (including *A. turgida*-present in the CRB) were attracted to dung, while other endogeics were not. Other categories of worms were not represented in the system.

Hutchinson and King (1980) examined the effects of sheep stocking rates on soil invertebrate populations, and Seastedt (1985) and Seastedt et al (1986) looked at the impact of clipping or mowing on soil arthropods. In general, these studies showed a peak of abundance at moderate plant defoliation levels. However, the results are not so clear with earthworms: Seastedt et al (1988) was inconclusive, but Todd et al (1992) found increased abundance of some species with increased mowing frequency, but no change (statistically insignificant declines of biomass) for other species. Consequently it appears that any assessment of the impact of various grazing management scenarios will have to be on a case-by case basis.

Soil compaction by animal activity (including humans) has variable effects on earthworm populations. Cuendet (1992) found contrasting effects of pedestrians on earthworms in two forest types, while Pizl's (1992) investigation of the effect of farm machinery on earthworms in orchards clearly demonstrated a negative effect on all earthworms. Different ecological categories of worms were affected to differing degrees in each case. More to the point, cattle trampling has a blanket negative effect that is less intense on large-bodied earthworms (Cluzeau et al 1992). In this study, trampling was very intense, such as would be found by gateways or at water sources.

All of the three effects of grazing considered here show variable effects by earthworm species and/or habitat type. Endogeic species often

suffered less than epigeics, and large species were also less heavily impacted. Without further knowledge of the native earthworms of the CRB and the presence/absence of earthworms in land subject to grazing in the CRB, it is not much use to speculate further.

Burning: James (1988) describes the impact of fire in Kansas tallgrass prairie on native earthworm populations. The effect was positive, since fire stimulates grass growth by allowing more rapid warming of the soil in the spring. In contrast, European species declined with burning, probably because they were less able to tolerate the higher soil temperatures on burned plots. Fire as a management tool thus may be anticipated to be short-term neutral or positive on native endogeic species where fire is a natural recurring element of the ecosystem. If the European invaders are near their temperature tolerance limits under fire-suppression conditions, they may be pushed to the limits in the post-fire environment. Obviously, anything that removes a litter layer and down logs could have a negative impact on epigeics. Additional information more relevant to forest fires is in Abbot (1984, 1985), though the work was done in jarrah forests of Australia.

Logging: The primary effects of tree removal on endogeic species would seem to be in the soil climate area, since surface and soil organic matter pools are probably sufficient to carry them through until second growth plants become established. If selective cutting practices are adopted, this impact would be moderated. Mechanical disturbance from heavy equipment may be the most deleterious (cf Schaefer et al 1990).

Epigeic species would be expected to suffer most from the loss of tree cover, since this would make their preferred microhabitat less hospitable and ultimately less abundant, with the loss of annual leaf input. There may be a short term increase from slash left on site, but it is difficult to say if the microclimate would remain suitable for earthworm activity.

The above is relevant to short term effects (1-10 years). Medium term and long term effects???

Literature Cited

Abbot, I. 1984. Changes in the abundance and activity of certain' soil and litter fauna in the Jarrah Forest of Western Australia after a moderate intensity fire. *Australian Journal of Soil Research* 22:463-469.

_____. 1985. Influence of some environmental factors on indigenous earthworms in the Northern Jarrah Forests of Western Australia. *Australian Journal of Soil Research* 23:271-290.

Bouche, M.B. 1977. Strategies lombriciennes. In: *Soil Organisms as components of ecosystems*. Ecological Bulletin (Stockholm) 25:122-132.

Cluzeau, D., F. Binet, F. Vertes, J.C. Simon, J.M. Riviere and P. Trehen. 1992. Effects of intensive cattle trampling on soil-plant-earthworms system in two grassland types. *Soil Biology and biochemistry* 24:1661-1665.

Cuendet, G. 1992. Effect of pedestrian activity on earthworm populations of two forests in Switzerland. *Soil biology and Biochemistry* 24: 1467- 1470.

Eisen, G. 1900. Researches in American Oligochaeta, with especial reference to those of the Pacific Coast and adjacent islands. *Proceedings of the California Academy of Sciences, San Francisco*. Third Series, 11(2):85-276.

Fender, W.M. 1985. Earthworms of the Western United States. Part I. Lumbricidae. *Megadrilologica* 4:93- 132.

Fender, W.M and D. McKey-Fender. 1990. Oligochaeta: Megascolecidae and other earthworms from western North America. In D.L. Dindal, editor. *Soil Biology Guide*. Wiley and Sons, New York.

Gates, G.E. 1967. On the earthworm fauna of the Great American Desert and adjacent areas. *Great Basin Naturalist* 27:142-176.

_____. 1977. On the correct generic name for some West Coast native earthworms, with aids for a study of the genus. *Megadrilogica* 3:54-60.

Hutchinson, K.J. and K.L. King. 1980. The effects of sheep stocking level on invertebrate abundance, biomass and energy utilization in a temperate sown grassland. *Journal of Applied Ecology* 17:368-387.

James, S.W. 1988. The **postfire** environment and earthworm populations in tallgrass prairie. *Ecology* 69:476-483.

_____. 1992. Localized dynamics of earthworm populations in relation to Bison dung in North American tallgrass prairie. *Soil Biology and Biochemistry* 24:1471-1476.

Kalisz, P.J. and D.B. Dotson. 1989. Land use history and the occurrence of exotic earthworms in the mountains of eastern Kentucky. *American Midland Naturalist* 122:288-297.

Langmaid, K.K. 1964. Some effects of earthworm invasion in virgin podsols. *Canadian Journal of Soil Science*. 44:34-37.

Lavelle, P. 1983. The structure of earthworm communities.. In J.E. Satchell, editor, *Earthworm ecology, from Darwin to vermiculture*. Chapman and Hall, London.

Lavelle, P. and A. Martin. 1992. Small-scale and large-scale effects of endogeic earthworms on soil organic matter dynamics in soils of the humid tropics. *Soil Biology and Biochemistry* 24:1491-1498.

Lee, K.E. 1959. The earthworm fauna of New Zealand. New Zealand Department of Scientific and Industrial Research Bulletin 130, 486 p.

_____. 1961. Interactions between native and introduced earthworms.

Proceedings of the New Zealand Ecological Society 8:60-62.

_____. 1985. Earthworms- their ecology and relationships with soils and land use. Academic Press. 41 lp.

Ljungstrom, P.-O. 1972. Taxonomical and ecological notes on the earthworm genus *Udeina* and a requiem for the South African acanthodriles. *Pedobiologia* 12: 100- 110.

McKey-Fender, D. 1970. Description of endemic earthworms from Eastern Oregon (Oligochaeta: Acanthodrilidae). *Northwest Science* 44:235-243.

McKey-Fender, D., W.M. Fender and V.G. Marshall. 1994. North American earthworms native to Vancouver Island and the Olympic Peninsula. *Can J. Zool.* 72:1325-1339.

Pizl, V. 1992. Effect of soil compaction on earthworms (Lumbricidae) in apple orchard soil. *Soil Biology and Biochemistry* 24: 1573-1576

Schaefer, D.J., T.R. Seastedt, D.J. Gibson, D.C. Hartnett, B.A.D. Hetrick, S.W. James, D.W. Kaufman, A.P. Schwab, E.E. Herricks, and E.W. Novak. 1990. Field bioassessments for selecting test systems to evaluate military training lands in tallgrass prairie. *Ecosystem Health.- V. Environmental Management* 14:81-93.

Seastedt, T.R. 1985. Maximization of primary and secondary productivity by grazers. *American Naturalist* 126:559-564.

Seastedt, T.R., D.C. Hayes and N.J. Petersen. 1986. Effects of vegetation, burning and mowing on soil macroarthropods of tallgrass prairie. In G.K. Clambey and R.H. Pemble, editors, *Proceedings of the Ninth north American Prairie Conference*. Tri-College Press, Fargo, ND.

Seastedt, T.R., S.W. James and T.C. Todd. 1988. Interactions among soil

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invertebrates, microbes and plant growth in the tallgrass prairie.
Agriculture, Ecosystems and Environment 24:219-228.

Smith, F. 1928. An account of changes in the earthworm fauna of Illinois and a description of one new species. *Illinois Natural History Survey Bulletin*. 17:347-362.

Todd, T.C., S.W. James and T.R. Seastedt. 1992. Soil invertebrate and plant responses to mowing and carbofuran application in a North American tallgrass prairie. *Plant and Soil* 144:117-124.

Wood, H.B. and S.W. James. 1993. Native and introduced earthworms from selected chaparral, woodland, and riparian zones in southern California. General Technical Report PSW-GTR-142. Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture; 20 p.